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Germination-Temperature Profiles for Achenes of Yellow Starthistle (*Centaurea solstitialis*)[1]

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Abstract: Yellow starthistle is an annual that is dependent on achene production, dispersal, and germination for stand renewal. Our purpose in this study was to determine the temperature relations for germination of achenes of this species. Germination temperature profiles were developed for achenes of yellow starthistle collected from 15 sites in California, Nevada, and Oregon. Each profile consisted of achene germination at 55 constant or alternating temperatures from 0 through 40 C. A total of 85 germination temperature profiles were developed by using the germination data to construct quadratic response surfaces through regression analysis. For most profiles, germination occurred at all the temperature regimes except a constant 40 C. This includes a constant 0 C and 0 alternating with 40 C. Rarely, there was no germination at 35 C and 35 C alternating with 40 C. The only evidence of afterripening requirements for achenes of yellow starthistle that we noted occurred at very cold temperature regimes. At those temperatures, the germination of dark-colored achenes without pappus increased 3 mo after harvest, and decreased for light-colored achenes with a pappus. No single temperature regime always supported optimum germination when all the profiles were combined. The most frequent optima was 2/20 C. Comparing all profiles for the Davis, CA, accession, there were 5 regimes (5 and 10 C cold periods alternating with 15 through 25 C warm periods) that always supported optimum germination. Light-colored achenes with pappus tended to have optimal germination at colder temperatures, and the dark-colored achenes at higher temperatures when seeds were tested immediately after harvest.

Nomenclature: Alfalfa, *Medicago sativa* L. #[3] MEDSA; tocalote, *Centaurea melitensis* L.; yellow starthistle, *Centaurea solstitialis* L. # CENSO.

Additional index words: Seedbed ecology, seedbed temperatures, optimum germination, invasive species.

INTRODUCTION

Yellow starthistle (*Centaurea solstitialis* L.) is a winter annual of Eurasian origin that is a widespread and serious weed in the western United States (Benefield et al. 2001; DiTomaso et al. 1999; Maddox et al. 1985; Roché 1965; Roché and Thill 2001). Universally, in the American literature, yellow starthistle is referred to as a facultative winter annual or simply as an annual (Keil and Turner 1993), but in the European literature, it is sometimes listed as a biennial (Tutin et al. 1964). The European distribution is given as southern Europe, with adventive populations widely scattered in Central Europe (Tutin et al. 1964).

Yellow starthistle was reported in the Sacramento Valley of California at Grand Island, Colusa County, about 1879 (Robbins 1940). The introduction in California is thought to be from contaminated alfalfa (*Medicago sativa* L.) seed (Gerlach 1997). Surprisingly, considering its current extreme abundance and dominance in California (it is estimated that infestations occur on between 15 and 22% of the surface area of the state [Balciunas and Villegas 1999]), yellow starthistle was not the first annual *Centaurea* species introduced to the state. Tocalote (*Centaurea melitensis* L.) was well established during the Mission period of California history (Hendry and Bellue 1925).

Yellow starthistle had spread to southwestern Oregon by the 1920s (Sheley et al. 1993). In apparently separate

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[3] Letters following this symbol are a WSSA-approved computer code from *Composite List of Weeds*, Revised, 1989. Available only on computer disk from WSSA, 810 East 10th Street, Lawrence, KS 66044-8897.

introductions in contaminated alfalfa seed, the exotic annual became established in southeastern Washington and adjacent Idaho (Gerlach 1997; Roché 1965).

In cismontane northern California, yellow starthistle germinates with the first biologically effective moisture event in the fall, grows as a rosette during the classic Mediterranean-type winter climate, and flowers the next summer. The microenvironmental parameters and population dynamics of such seedbeds have been described in detail (Evans et al. 1975; Joley et al. 2003; Young et al. 1973; Young et al. 1991). Yellow starthistle is well established in the western Great Basin in a much colder and more arid environment than cismontane California. In the Great Basin environment, successful exotic weeds often have the potential to germinate in seedbed temperatures at or near 0 C (Young et al. 1968).

Yellow starthistle only propagates by seed germination and seedling establishment. Obviously, seed production, dispersal, germination, and seedling establishment are essential aspects of the invasive ecology of this weed. The plumed achenes (seeds) of yellow starthistle are 2- to 2.5-mm long, with a 4-mm pappus, and they weigh about 1.9 mg. Achene production per plant has been measured at 700 to 10,000 (Roché and Thill 2001). Generally, about 1,000 achenes are produced per plant, with markedly greater production being rare. Yellow starthistle infestations have been reported to produce 250 million achenes/ha annually (Callihan et al. 1993). The pappus apparently functions as a means of orienting the achene with the seedbed for optimum germination, rather than as an aid in wind dispersal (Roché and Thill 2001). Most achenes are dispersed relatively close to the plant. Roché (1991) found that 92% of the yellow starthistle achenes were recovered from traps located 0.6 m from the plants on which they were produced.

Despite this limited dispersal distance, the rate of invasion by yellow starthistle is phenomenal. In southeastern Washington, yellow starthistle infestation increased from 60 to 4,000 ha from 1954 to 1964 (Roché 1965).

Yellow starthistle has two types of achenes that develop in each capitulum (flower head) (Joley et al. 1997; Roché 1965). The occurrence of two or more morphologically distinct achenes (heteromorphism) on the same plant is common in the Asteraceae (Harper 1997; Olivieri and Berger 1985). Floret and achene development occurs centripetally (from without, proceeding toward the center) (Maddox et al. 1996). Florets that open first along the periphery of the receptacle (ray flowers) are sterile. This is characteristic of the *Centaurea* in North America (Keil and Turner 1993).

Peripheral florets of the disk develop into achenes that are usually dark brown (black) and lack pappus bristles. Apparently because these achenes are located on the outside of the receptacle and pressed by the subtending phyllaries (bracts) that enclose the flower head, the dark achenes are often asymmetrical in shape. Joley et al. (1997) reported that these achenes tend to remain in the seed head at maturity and are not dispersed until the plants are completely mature and the subtending bracts reflex or break away from the receptacle. In contrast, the florets located in the central portion of the receptacle develop achenes that are light brown to tan and have a persistent pappus with unequal length bristles. These achenes are dehisced during the summer. Maddox (1981) gives the ratio of pappus to nonpappus achenes as ranging from 3.4:1 to 8.7:1. Benefield et al. (2001) reported that of yellow starthistle seed heads examined in a study conducted in California, 85% of the achenes produced per head were the light-colored form with a pappus, and 15% were the dark form without pappus (5.7:1). Roché and Thill (2001) gave the ratio between light-colored achenes with pappus to dark-colored without pappus as 3:1.

Maguire and Overland (1959) obtained 100% germination of yellow starthistle achenes in darkness at 20 C but reported that at some temperatures, incubation in the light was better than in darkness. Roché (1965) determined that the achenes of yellow starthistle were generally nondormant and would germinate over a wide range of temperatures. He conducted his experiments under unspecified light conditions but unintentionally exposed them to unfiltered ambient light.

The most sophisticated germination experiments with yellow starthistle achenes have been done by D. B. Jolley and D. M. Maddox in California (Joley et al. 1992, 1997, 2003). They initially investigated the influence of light, temperature, achene type, collection date, dormancy, and storage time on the germination of yellow starthistle achenes. They found some germination in the dark but much higher germination with light. They considered that the achenes of yellow starthistle were sensitive to the quality of light to which they were exposed (Borthwick et al. 1954). Maximum germination of nearly 100% was obtained at 10, 15 and 20 C and at alternating temperatures of 5 C for 16 h and 15 C for 8 hours in each 24 h. Germination of achenes with pappus was higher than for nonpappus achenes.

A very important aspect of the biology of yellow starthistle is that the individual florets largely require cross-fertilization to produce achenes (Maddox et al. 1996).

Table 1. Sites where yellow starthistle achenes were collected for germination experiments.[a]

Location	Years collected	Separate achene trials	Afterripening test conducted
Davis, CA	1993	No	No
	2000	Yes	Yes
	2001	Yes	Yes
	2002	Yes	Yes
Brown's Valley, CA	1993	No	No
	2000	Yes	No
Dana, CA	2000	Yes	Yes
	2001	Yes	Yes
	2002	Yes	Yes
Cassel, CA	2000	Yes	Yes
	2001	Yes	Yes
	2002	Yes	Yes
Clayton Valley, CA	1994	No	No
	2000	Yes	Yes
	2001	Yes	Yes
	2002	Yes	Yes
Montague, CA	1994	No	No
	2000	Yes	No
	2002	Yes	Yes
Mendocino, CA	1993	No	No
Scott Valley, CA	2002	Yes	Yes
Scott River, CA	2002	Yes	Yes
Jacksonville, OR	2002	Yes	Yes
Valley Rd., Reno, NV	2000	Yes	Yes
	2001	Yes	Yes
Sutro, Reno, NV	2002	Yes	Yes
Fort Hunter Liggett, CA	2000	Yes	No
Rohnert Park, CA	2001	Yes	Yes
San Benito County, CA	2000	Yes	No

[a] Separate achene trials refer to complete profiles being conducted with both dark achenes without pappus and light achenes with pappus. Afterripening refers to test conducted immediately after harvest and again after 3 mo.

This results in most populations being highly heterozygous (Sun 1997; Sun and Ritland 1998).

Our purpose was to determine the germination of yellow starthistle achenes at a wide range of constant and alternating temperatures.

MATERIALS AND METHODS

This research started in 1994 with seeds supplied by the late Charles Turner (Table 1). After his untimely death, work remained in abeyance until a new group of interested cooperators emerged in 2000. When the project was restarted, we collected from Turner's original sites and several additional locations (Table 1). We tried to obtain achenes from the same site for 3 consecutive years, but drought, herbicide applications, and the success of biological control agents (insects) interfered with these efforts at some locations (Table 1). For each collection site, inflorescences were clipped from 50 to 100 plants and returned to the laboratory where they were allowed to reach moisture equilibrium. Achenes were recovered by hand threshing, then cleaned with an air screen, and stored in paper bags at room temperature until germination tests were conducted. Initial tests were conducted as soon after collection as possible and repeated 3 mo after collection. For some sources, where achenes were supplied by other collectors, an immediate after-harvest test was not possible (Table 1). Except for the initial achenes collected by Charles Turner, we ran separate tests at each date for dark-colored achenes without pappus and light-colored achenes with pappus. In all, 85 germination profiles were conducted, with achenes collected from 15 different locations in 3 states, for a total of 588,500 achenes tested.

In all experiments, four replications of 25 achenes each were used. Achenes were placed on top of nontoxic commercial germination paper in closed Petri dishes and kept wet with tap water. Initial wetting and moisture imbibition took place in darkness. Germination trials were conducted in the dark. Achenes were considered germinated when the radicle emerged 5 mm. Germination counts were made after 1, 2, and 4 wk. Constant incubation temperatures were 0, 2, and 5 C and at 5 degree increments through 40 C. Alternating regimes included 16 h at each constant temperature, plus 8 h at each possible higher temperature per 24 h. For example, 35 C alternated with 40 C only, whereas 0 C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40 C. This made a total of 55 constant and alternating temperature regimes (Young et al. 1970, 1973, 1991).

The germination responses of the accessions of yellow starthistle were compared using the following categories of seedbed temperature regimes (Young and Evans 1982):

1. Very cold: 0/0 (constant 0 C), 0/2 (0 C for 16 h and 2 C for 8 H in each 24 h), 0/5, and 2/2 C;
2. Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10 C;
3. Cold fluctuating: 0/20 through 0/40 C and 2/20 through 2/40 C;
4. Fluctuating: 5/35, 5/40, 10/35, 10/40, and 15/40 C;
5. Moderate: 5/20 through 5/40, 10/10 through 10/30 C, 15/15 through 15/35 C, 20/20 through 30/35 C, and 25/25 through 25/30 C;
6. Warmer: 20/40. 25/35, 25/40, 30/30 through 30/40, 35/35, 35/40, and 40/40 C.

The temperature categories reflect germination environments of field seedbeds based on several years of monitoring (Evans and Young 1970, 1972; Evans et al. 1970).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 0.01 level of probability (Evans et al.

Table 2. Germination parameters calculated from quadratic-response surfaces (Young and Evans 1982).

Parameters	Derived parameters	Purpose
Calculated within profile:		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination	Number with germination divided by 55	Indication of breadth of germination response
Percentage of regimes with optimum germination	Number of regimes with germination not less than maximum observed minus one-half confidence interval divided by 55	Provides indication of the breadth of temperatures that support optimum germination
Mean of optima temperatures	Sum of optima divided by number of optima regimes	Provides measure of potential germination at adapted temperatures
Maximum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles:		
Frequency of optima	Times temperature regime supports optima divided by total number of profiles	Provides an estimate of germination with precision

1982; Palmquist et al. 1987; Young et al. 1980). Several germination parameters were calculated from the quadratic response surfaces (Table 2) (Young and Evans 1982). Among profiles, individual parameters were compared by analysis of variance and the use of Duncan's New Multiple Range Test to separate means.

RESULTS AND DISCUSSION

Davis, CA, Collections. We started with the accession of yellow starthistle achenes from Davis, CA, because of the 4 yr of germination-temperature profiles available and the Sacramento Valley location of the collection site where yellow starthistle has been established for more than a century (Tables 3 and 4). It is apparent from the profile (Table 3), that some germination occurs at all temperatures tested except a constant 40 C. This includes a constant 0 C and 0 C alternating with 40 C. On given years and types of achenes (pappus vs. no pappus), the number of regimes that support some germination drops, but it is usually 35 and 35/40 C that fail to have any germination in addition to a constant 40 C. Note that for the 7 profiles completed for this location, the percentage of the 55 temperatures that supported some germination never dropped below 94% and the average was 96% (Table 4). The maximum observed germination for the achenes collected at Davis ranged from 96 to 100% and averaged 99% (Table 4). The mean of the optima was 96% and on average, 20% of the temperatures supported optimum germination (Table 4). The mean germination for the profile averaged 55%. Only having roughly 50% of the 5,500 achenes tested in each profile germinate may seem low, but remember the profile includes extremely low, high, and fluctuating temperature regimes, and our experience with some 800 germination-temperature profiles is that 50% mean germination is very high.

For a winter annual species that has to germinate in the fall, there is nothing limiting about the germination profile of achenes of yellow starthistle in terms of some germination occurring. For many successful, exotic an-

Table 3. Mean germination ± one-half of the confidence interval at the 0.01 level of probability for achenes of yellow starthistle collected at Davis, CA, in 1993. In this early test, achenes were not separated on the basis of color and pappus persistence.[a, b]

Cold period temperatures	Germination at warm period temperatures (C)									
	0	2	5	10	15	20	25	30	35	40
C	%									
0	15 ± 5	18 ± 6	80 ± 4	84 ± 4	[96 ± 4*]	86 ± 4	86 ± 4	70 ± 6	50 ± 8	20 ± 10
2		20 ± 8	80 ± 6	90 ± 4	94 ± 4*	94 ± 4*	95 ± 4*	91 ± 6	80 ± 8	40 ± 8
5			76 ± 8	90 ± 4	94 ± 4*	94 ± 4*	95 ± 5*	91 ± 6	80 ± 8	40 ± 8
10				84 ± 4	90 ± 4	88 ± 6	92 ± 6*	90 ± 4	82 ± 8	52 ± 8
15					80 ± 6	86 ± 6	92 ± 4*	93 ± 6*	90 ± 6	60 ± 6
20						95 ± 4*	90 ± 6	88 ± 6	86 ± 6	42 ± 8
25							86 ± 6	82 ± 6	74 ± 6	36 ± 8
30								68 ± 8	42 ± 8	32 ± 8
35									10 ± 10	8 ± 12
40										0 + 14

[a] Number following the mean is one-half of the confidence interval as determined from regression equations used to develop the response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by [ ].

[b] * indicates means not lower than the maximum germination minus one-half of its confidence interval, our definition of optimum germination.

Table 4. Comparison of germination-temperature profiles for achenes of yellow starthistle collected near Davis, CA.

Germination parameters	1993	2000 No pappus	2000 Pappus	2001 No pappus	2001 Pappus	2002 No pappus	2002 Pappus	Mean
	(%)							
Profile characteristics								
Mean	64 a	57 ab	49 b	60 ab	52 b	52 b	52 b	55
Regimes with germination	98	96	98	94	96	94	94	96
Mean of optima	94	98	94	100	96	93	92	96
Regimes with optima	20 c	6 d	25 bc	16 cd	29 ab	29 ab	38 a	20
Maximum	96	100	100	100	100	99	99	99
Seedbed temperatures								
Very cold	33 a	10 b	40 a	33 a	8 b	15 b	16 b	22
Cold	90 a	40 c	88 a	55 bc	63 b	87 a	78 a	72
Cold fluctuating	71 ab	63 bc	74 ab	65 bc	69 abc	78 a	59 c	68
Fluctuating	63 b	78 a	61 bc	84 a	50 cd	35 e	45 c	59
Warmer	35 b	34 b	45 a	37 ab	36 ab	22 c	31 bc	30
Moderate	89 ab	70 c	92 a	87 abc	85 abc	77 bc	84 abc	83

[a] Means (within rows) followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's New Multiple Range Test. No letters indicate no significant differences.

nual species, the seed production potential is so much greater than that required to perpetuate the population, some germination at less than optimum temperatures often may be all that is required (Young et al. 1968). There is a second aspect to seed production greatly in excess of that required to perpetuate populations of annuals. Fruits (achenes) or seeds that find themselves in a seedbed situation outside their inherent potential for germination, may acquire dormancy, which allows the building of seed banks even when the propagules originally produced were highly germinable (Joley et al. 2003; Young et al. 1968). With a reported potential achene production of 700 to 10,000 per plant (Roché and Thill 2001) and limited dispersal of the achenes (Roché 1991), yellow starthistle obviously produces many more achenes per plant than necessary to renew the existing population, or there are safe sites in the seedbed to support germination. Lastly, in the Mediterranean climate of cismontane California and southwestern Oregon, there is an extreme selective value associated with being first to germinate when the initial biologically effective moisture event occurs in the fall (Young et al. 1981).

Table 5. Summary of 48 germination-temperature profiles for achenes of yellow starthistle from 14 collection sites. For each accession, profiles were run for dark-colored achenes without pappus and for light-colored achenes with a pappus.[a]

Germination parameters	Achenes With pappus	Achenes Without pappus
	(%)	
Profile characteristics		
Mean	64 a	55 b
Regimes with some germination	94	94
Mean of optima	97	95
Regimes with optima	28	17
Maximum	99	99
Seedbed temperatures		
Very cold	56 a	
Cold	84	71
Cold fluctuating	73	64
Fluctuating	50	51
Warmer	33	27
Moderate	88	81

[a] Means (within rows) followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's New Multiple Range Test. No letters indicate no significant differences.

Pappus vs. Nonpappus Achenes. Since Roché (1965) described the occurrence of morphologically different achenes of yellow starthistle in the same flower head, there has been considerable discussion of the biological significance of the observation. Joley et al. (1997) reported marked differences in the germination of dark-colored achenes without pappus vs. lighter-colored achenes with pappus. We compared the germination of the two forms of achenes in 48 germination profiles (264,000 achenes) collected from 14 locations in California, Oregon, and Nevada (Table 5). The overall mean germination of dark achenes without pappus was significantly ($P \geq 0.01$) lower than for lighter-colored achenes with pappus. The difference in mean germination was largely attributable to lower germination by the dark achenes without pappus at the 4 temperature regimes we characterized as very cold seedbed temperatures (Table 6). There was no significant ($P \geq 0.01$) difference in germination of the morphologic types at 0 C, where limited germination occurred, but at the alternating temperatures of 0/2, 0/5, and at a constant 2 C, the germination of the dark achenes without pappus was 38, 53, and 38% lower, respectively.

Table 6. Comparison of germination of achenes of yellow starthistle with and without pappus at the 4 temperatures that constitute the very cold category of seedbed temperatures. Data condensed from 48 germination profiles from accessions collected at 14 sites. Incubation regimes are constant for single digit temperatures and 16 h at the lower and 8 h at the higher in each 24-h period for the temperatures separated by a slash mark.[a]

Incubation temperature	Achenes	
	With pappus	Without pappus
C	(%)	
0	25	14
0/2	65 a	27 b
0/5	88 a	35 b
2	69	31

[a] Means (within rows) followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's New Multiple Range Test. No letters indicate no significant differences.

In interpreting these differences, it is important to remember that the light-colored achenes with pappus are dispersed first and the dark-colored achenes without pappus may not be dehisced from the seedhead until complete maturity of the plants and wind action (as with the first biologically effective moisture event of the autumn) occurs (Joley et al, 1997).

Afterripening of Yellow Starthistle Achenes. Afterripening is usually considered to be caused by seed embryos being immature when the seed or fruit dehisces from the plant. Over a period of time after maturity, the embryos gradually mature, and this maturation is independent of the environment where the seeds reside (Mayer and Poljakoff-Mayber 1953). The results of early trials with freshly harvested achenes of yellow starthistle universally indicated that the achenes would germinate and germinate at relatively high levels at the incubation temperature regimes that were used (e.g., Roché 1965). Based on these results it was assumed that achenes of yellow starthistle did not have afterripening requirements.

We have the at-harvest vs. 3-mo-postharvest comparison results from 36 germination temperature profiles from 10 different locations (Table 7). At some sites, we have this comparison for more than 1 yr. This data set differs from the total data set because we received some accessions later than 3 mo after harvest. The only marked differences in these comparisons occurred at what we define as very cold seedbed temperatures (Table 7). For light-colored achenes with a pappus germination was significantly ($P \leq 0.01$) lower 3 mo after harvest and with dark achenes without pappus the reverse was true. The germination of dark-colored achenes without pappus was not as high 3 mo after harvest as that of the light-colored achenes with pappus at maturity.

Table 7. Summary of 36 germination-temperature profiles for achenes of yellow starthistle from 10 collection sites for germination at collection time (harvest) and at least 3 mo later (afterripening). For each accession, profiles were run for achenes that were dark colored without a pappus and for achenes light in color with a pappus.[a]

Germination parameters	Achenes			
	With pappus		Without pappus	
	Harvest	Afterripening	Harvest	Afterripening
	(%)			
Profile characteristics				
Mean	65	63	55	56
Regimes with some germination	94	94	94	94
Mean of optima	97	92	95	97
Regimes with optima Maximum	99	97	99	99
Seedbed temperatures				
Very cold	56 a	41 b	24 c	44 b
Cold	82	80	71	68
Cold fluctuating	76	78	65	64
Fluctuating	56	57	55	51
Warmer	30	34	30	31
Moderate	92	88	82	79

[a] Means (within rows) followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's New Multiple Range Test. No letters indicate no significant differences.

Optimum Temperatures for Germination. No single temperature regime always supported optimum germination when all the germination temperature profiles for yellow starthistle are combined (Table 8). Not only did a single temperature not always support optimum germination, the most frequent temperature for optima was 2/20 C and that was only 57% of the time. In interpreting these data, remember that the maximum germination observed for most profiles was often 96 to 100% with usually a narrow confidence interval. This means that when one examines the data presented in Table 8 and 6% of the total profiles conducted had optima at 0/5 C, it is apparent that a very high level of germination occurred

Table 8. Frequency with which a given temperature supported optimum germination. Data are based on all germination-temperature profiles conducted with profiles for the two types of achene morphology combined.

Cold period temperatures	Frequency of optima									
	0	2	5	10	15	20	25	30	35	40
C	%									
0			6	20	47	53	47	20		
2				20	43	57	53	33	7	
5				13	33	53	27	23	7	
10				3	37	53	53	40	10	
15					23	37	47	53	17	3
20						13	27	23	13	3
25							3	17		
30								3		
35										
40										

Table 9. Frequency with which a given temperature supported optimum germination from achenes of yellow starthistle collected from the same stand at Davis, CA. Data are based on all germination-temperature profiles conducted with profiles for the two types of achene morphology combined.

Cold period temperatures	Frequency of optima									
	0	2	5	10	15	20	25	30	35	40
C	%									
0					43	28	71	57		
2					71	71	71	14		
5					100	100	100	28		
10					100	100	100	14		
15					57	57	86	28	14	
20						71	43	14	14	
25										
30										
35										
40										

Table 10. Frequency that a given temperature supported optimum germination. Data are based on all germination-temperature profiles conducted with light-colored achenes with pappus.

Cold period temperatures	Frequency of optima									
	0	2	5	10	15	20	25	30	35	40
C	%									
0			13	38	75	69	50	25		
2			13	31	63	63	69	31	13	
5				25	38	63	45	31	6	
10				6	50	63	69	38	13	
15					31	38	56	56	19	
20						25	45	38	13	
25								21		
30								6		
35										
40										

at least occasionally at this cold temperature. Is there a dormancy of yellow starthistle achenes that is broken by prechilling? In classical seed technology, this would be determined by prechilling achenes at a constant incubation temperature that inhibits germination and then transferring the achenes to a higher incubation temperature. There is no 0 C or above cold temperature that completely inhibits germination of achenes of yellow starthistle. Achenes of yellow starthistle incubated at temperature regimes above the self prechilling level (0 through 5 C) will produce 100% germination, so prechilling is not required.

A large proportion of the temperature regimes that supported optimum germination (31%) occurred at regimes with cold period temperatures of 5 C or lower. This temperature range falls within the generally accepted level for breaking dormancy by satisfying prechilling (stratification) requirements (Mayer and Poljakoff-Mayber 1953). The cold period base temperature with the highest percentage of optima is 2 C (41% of total). The base warm period temperatures that supported the highest frequency of optima were 15, 20, and 25 C (37, 44, and 37%, respectively) (Table 8).

The constant temperatures of 10 through 35 C supported optimum germination, but only at a mean frequency of 9% (range 3 to 23%) (Table 8). At any given base cold or warm period temperature where optimum germination occurred, the frequency of optima was much higher with alternating vs. constant incubation temperatures.

Optimum Temperatures for Germination from Repeated Collections from the Same Stand. In contrast with the data set for all the temperature germination profiles conducted (Table 8), comparing repeated collections from the same stand located at Davis, CA, produced a more compact and specific array of regimes supporting optima (Table 9). These are the same accessions of yellow starthistle used in Table 4 where average germination of optima was 99%. There were 5 temperatures (5 and 10 C cold period and 15 through 25 C warm period temperatures) that always supported optimum germination.

Achene Morphology and Germination Optima. Comparing the frequency of optima for germination temperature profiles for the two types of yellow starthistle seed morphology reveals a tendency for optima for light-colored achenes with pappus to have optima at colder incubation temperatures and dark-colored achenes without persistent pappus to shift to warmer temperatures (Tables 10 and 11). For example, the dark-colored achenes without pappus had no optima occurring at regimes with 5 C warm periods and only 7% of the profiles had optima with regimes with 10 C warm periods (Table 11). With 0 C cold period temperatures and warm period temper-

Table 11. Frequency that a given temperature supported optimum germination. Data are based on all germination-temperature profiles conducted with dark-colored achenes without pappus.

Cold period temperatures	Frequency of optima									
	0	2	5	10	15	20	25	30	35	40
C	%									
0					14	36	43	14		
2				7	21	50	36	36		
5					20	43	7	14	7	
10					21	43	36	43	7	
15					7	36	36	50	14	7
20							7	7	14	7
25							7	14		
30								3		
35										
40										

atures from 15 through 30 C, the light-colored achenes with pappus average 55% optimum germination, and the dark-colored achenes without pappus averaged only 27% (Tables 10 and 11). The dark-colored achenes without pappus had optima at regimes with warm period temperatures of 40 C, and the light-colored achenes did not.

Perspective on Germination of Yellow Starthistle Achenes. Although the data set presented in this study is quite large, it is only preliminary in terms of fully understanding the seed and seedbed ecology of the achenes of yellow starthistle. This study provides a comprehensive model of the germination response of dimorphic achenes of yellow starthistle to seedbed temperatures in the near absence of light. The absence of light means burial in the soil or dense litter. No one has shown that biologically significant light for seed germination penetrates any soil coverage. For a broad range of temperatures, there is little room for enhancement because our study indicates optimum germination at or near 100%. However, the work of Joley et al. (2003) indicates that far-red light may reduce or inhibit the germination of achenes of yellow starthistle.

The potentially huge annual seed rain of yellow starthistle that vastly exceeds levels necessary to renew populations of this weed and the reported limited dispersal distance of these seeds, suggests a vast over abundance of achenes in the seedbed. This over abundance potentially interacts with control strategies for the species in two ways. Research by Joley et al. (2003) indicates that germination of yellow starthistle achenes in the seed bank is cyclic with reduced germination in the spring and summer and increased germination in the fall. First, biological control strategies have concentrated on the introduction of insects that are seed predators (Balciunas and Villegas 1999). This may be an effective strategy, but the overabundance of seed production means the predator population must reach very high levels to be effective. Secondly, the production and dispersal of more seeds than there are safe sites for germination in a given seedbed, often leads to the acquiring of seed dormancy by seeds that are not dormant at maturity (Young et al. 1968). Essentially, this acquired dormancy allows the species to have the ecological advantages of both simultaneous and continuous germination. This obviously leads to the development of persistent seed banks that greatly complicates weed suppression.

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